Great Basin Naturalist 52(3), pp. 262–268

POST-PLEISTOCENE DISPERSAL IN THE MEXICAN VOLE (*MICROTUS MEXICANUS*): AN EXAMPLE OF AN APPARENT TREND IN THE DISTRIBUTION OF SOUTHWESTERN MAMMALS

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ABSTRACT.—The present distribution of the Mexican vole (*Microtus mexicanus*) is not entirely the product of post-Pleistocene forest fragmentation and extinction; recent dispersal also is indicated. Literature records further suggest that this phenomenon may reflect a general pattern of northward range expansion in many southwestern mammal species.

Key words: Microtus, *vole, dispersal, biogeography, vicariance, Pleistocene.*

Traditional biogeographic theory attributes the modern distribution of small, nonflying montane mammals in the Southwest to post-Pleistocene climatic change (Brown 1971, 1978, Patterson 1984, Patterson and Atmar 1986). Restriction of woodland and forest habitat to higher elevations is assumed to have stranded such species on isolated patches of montane habitat. Although it is recognized that local extinction has caused further range reductions, post-Pleistocene range expansion generally has been discounted (Brown 1971, 1978). This relict model satisfactorily explains the distribution of many Great Basin species, but evidence from elsewhere in the Southwest strongly supports recent dispersal (Davis and Dunford 1987, Davis and Ward 1988, Davis et al. 1988, Davis and Bissell 1989, Davis and Brown 1989, Lomolino et al. 1989).

In this paper we will review evidence indicating that many southwestern mammals—including the Mexican vole and other montane mammals, as well as nonmontane species—have shown a striking northward range shift during the past several decades. For some species this pattern appears to reflect milder winters or human influences; for others the trend is harder to explain. If verified, however, this trend presupposes (among other things) a greater dispersal capability than is typically attributed to small mammals.

DISPERSAL: A BRIEF REVIEW

Post-Pleistocene dispersal has been verified primarily in (1) conspicuous, diurnal mammals such as sciurids and (2) mammals colonizing regions that were previously well sampled by collectors. For species and groups that do not fall into either category, the biogeographer is left to interpret broader distribution patterns and/or small bits of indirect evidence.

As an example of the first situation, Davis and Brown (1989) and Davis and Bissell (1989) showed that recent dispersal has significantly altered the distribution of Abert's squirrel (*Sciurus aberti*). Another example involves the dusky chipmunk (*Tamias obscurus*), which was absent from Thomas Mountain in southern California at least between 1974 and 1976 (Callahan 1977). By 1979 the species had recolonized this peak, which is isolated from the San Jacinto range by a 10-mile stretch of semiarid grassland/sagebrush habitat (Callahan, in preparation). The second scenario is illustrated by Davis and Dunford (1987) and Davis and Ward (1988), who found evidence of recent montane colonization by *Sigmodon ochrognathus* in a well-studied area of southeast Arizona.

Since many small mammals are not readily trapped and many localities have not been sampled extensively, it is easy for critics to "shoot down" new distribution records on the grounds of inadequate prior sampling. In such cases it is

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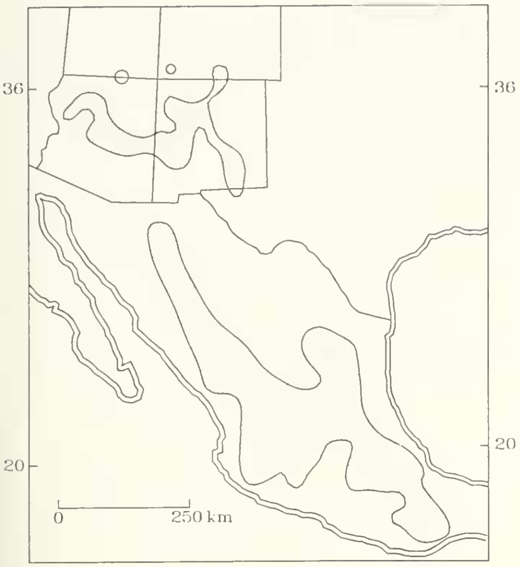

Fig. 1. Distribution of *Microtus mexicanus*. At this scale, only the two most isolated populations in the United States are distinguished (modified from Findley et al. 1975, Hall 1981, Finley et al. 1986, Hoffmeister 1986).

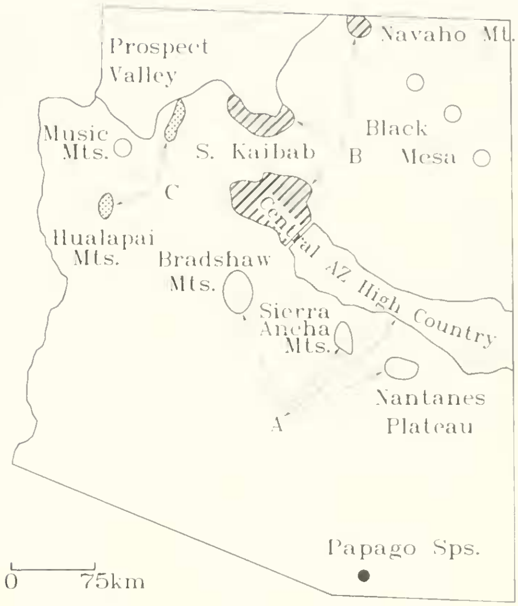

Fig. 2. Details of the distribution of *Microtus mexicanus* in Arizona showing isolated populations and three subspecies A, B, and C (modified from Hoffmeister 1986). Open circles indicate records added by Spicer et al. (1985) and Spicer (1987); subspecific relationships of these populations are unknown. Papago Springs is a late Pleistocene fossil site which includes a tentative record for this species (Harris 1985).

necessary to look at broader distribution patterns and draw some reasonable inferences. Davis et al. (1988) analyzed southwestern montane mammal distributions and found that distance from the source was a significant predictor of species richness—a relationship suggesting dispersal. Lomolino et al. (1989), in a study encompassing much of the Southwest, confirmed the relationship between species richness and isolation, and proposed recent dispersal by several montane species including *Microtus mexicanus*.

MEXICAN VOLE DISTRIBUTION

The range of the Mexican vole (Fig. 1) presently extends from Mexico into Arizona, New Mexico, southern Colorado, and Utah (Durrant 1952, Armstrong 1972, Findley et al. 1975, Hall 1981, Hoffmeister 1986). The species typically inhabits meadows in ponderosa pine and mixed conifer forests, but can occupy pinyon-juniper woodland if suitable understory is present (Harris 1985, Hoffmeister 1986). In Arizona it occurs less often in interior chaparral and Great Basin desertscrub (Hoffmeister 1986).

The late Pleistocene distribution of this species probably was continuous from the Mexican Plateau to the southwest U.S. (Findley and Jones 1962). Harris (1985) questions a fossil record from southeast Arizona that would confirm this past distribution, but the present disjunct range of the species (Fig. 1) implies its former presence in southeast Arizona regardless of the fossil record. Post-Pleistocene climatic changes fragmented this distribution, and local extinctions in southeast Arizona apparently separated the Mexican and northern populations. This scenario is consistent with the historical legacy hypothesis, but there is also evidence that the pattern has been modified by recent dispersal as discussed below.

EVIDENCE FROM ARIZONA.—The Mexican vole now occurs in the continuous forests of central Arizona and on isolated mountains to the south, southwest, and north (Figs. 1, 2). Four populations occur on mountains connected to the central high country by pinyon-juniper woodland and interior chaparral (Brown and Lowe 1983), through which the species could disperse: the Nantanes Plateau, the Sierra Ancha, the Bradshaw Mountains, and the South Kaibab (Fig. 2). Three other populations occur at sites that are isolated by grasslands but

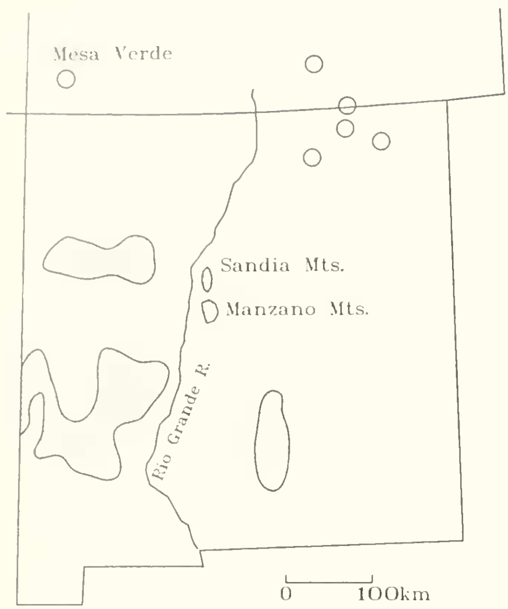

Fig. 3. Details of the distribution of *Microtus mexicanus* in New Mexico and southern Colorado showing some isolated populations (modified from Findley et al. 1975; some data from Hall 1981). Open circles indicate records listed by Finley et al. (1986).

interconnected by pinyon-juniper woodland and interior chaparral: Prospect Valley, the Music Mountains, and the Hualapai Mountains (Fig. 2).

Since the Hualapai Mountains and Prospect Valley still contain small patches of forest, the vole populations at these sites might be Pleistocene relicts in forest refugia. But the population in the Music Mountains, a site midway between the other two, consists of only pinyon-juniper woodland (Spicer et al. 1985). This habitat interconnects all three localities and is more likely to serve as a dispersal corridor than as a post-Pleistocene refugium. The species was recorded in the Hualapai Mountains in 1923 and in Prospect Valley in 1913, but it was not found in the Music Mountains until 1981 (Spicer et al. 1985).

When the rate of dispersal exceeds that of extinction, a species should be present on those montane islands closest to the source, assuming the species can cross the intervening habitat (MacArthur and Wilson 1967). The distribution of the Mexican vole in the Southwest generally fits this model (Fig. 2, Lomolino et al. 1989). In Arizona the most closely related isolate populations occur in geographic proximity (Hoffmeister 1986). Recent dispersal is not the only possible explanation for this pattern, but it is the most parsimonious one; ancient relicts in dissimilar habitats would be expected to show more evidence of divergence after several thousand years.

There is evidence of a recent range expansion in northeast Arizona. The Mexican vole was first recorded in the Navajo Mountains in southern Utah and northern Arizona in 1933 (Benson 1935). Although this locality seems isolated, since 1986 the species has turned up at several other sites on Black Mesa in northeast Arizona (Spicer 1987). These sites fall on a line southeast from Navajo Mountain to the southwest foothills of the Chuska Mountains.

At Black Mesa (Fig. 2) the habitat is pinyon-juniper, with ponderosa pines and a few Douglas-firs on north-facing slopes, draws, and other protected areas (Spicer 1987). Again, this is relatively poor habitat for this species, and it seems unlikely that the population could have survived in isolation for several thousand years. Between these sites and Navajo Mountain is mostly pinyon-juniper, with narrow strips of northern grassland and Great Basin desertscrub (Brown and Lowe 1983). The Mexican vole occupies these habitats elsewhere and presumably can disperse through them. This scenario implies that the Chuska Mountains, now unoccupied by the species (Hoffmeister 1986), will eventually be colonized (or recolonized) from the northwest.

EVIDENCE FROM NEW MEXICO AND COLORADO.—Findley et al. (1975) suggested that the range of *Microtus mexicanus* in New Mexico could have expanded as a result of recent dispersal. In the Sandia Mountains, trapping from 1950 to 1970 revealed only *M. longicaudus*. Mexican voles were first taken there in 1970 and soon became the dominant species. While the species could have been overlooked earlier, dispersal from the Manzano Mountains (Fig. 3) is an equally likely scenario. Until 1975 these were the northernmost records east of the Rio Grande River in New Mexico. The Mexican vole has since been recorded from five sites in extreme northeast New Mexico (Dalquest 1975, Finley et al. 1986).

In Colorado the first specimens were taken in 1956 at Mesa Verde (Rodeck and Anderson 1956). Later the species was found at seven more Colorado sites (Fig. 3; Mellott and Choate 1984, Finley et al. 1986). A trapping study in

TABLE 1. Southern mammal species for which there is evidence of a recent northward range expansion. Unless indicated otherwise, evidence is based on directionality and chronology of records: 1, Arizona distribution in Cockrum (1960) vs. Hoffmeister (1986); 2, distribution in Hall and Kelson (1959) vs. Hall (1981); 3, Texas distribution in Taylor and Davis (1947), Davis (1960), and Davis (1974). Nomenclature follows Jones et al. (1986).

Species	Region and direction of expansion	Evidence and References
Didelphis virginiana	N through E U.S.; N into S Arizona from N Mexico	Udvardy (1969), McManus (1974); Y. Petryszyn (personal communication)
Mormoops megalophylla	N in Texas	3; Taylor and Davis (1947); Davis (1960); Davis (1974); Mollhagen (1973)
Choeronycteris mexicana	Now a winter resident in S Arizona	R. Sidner (personal communication), probably due to hummingbird feeders
Leptonycteris sanborni	Now a winter resident in S Arizona	R. Sidner (personal communication), probably due to hummingbird feeders
Lasiurus ega	N in Texas	Spencer et al. (1988)
Idionycteris phyllotis	N in SW U.S. to Utah	First U.S. record was in 1955 in SE Arizona (Cockrum 1956); 2
Tadarida femorosacca	N in Arizona	1 and 2
Tadarida macrotis	N in Arizona; also Texas?	1; Mollhagen (1973)
Dasypus novemcinctus	N from S Texas into Oklahoma, Colorado, Kansas, and Nebraska	Buchannan and Talmage (1954); Udvardy (1969); Humphrey (1974); Meaney et al. (1987)
Lepus alleni	Limitedly NE in Arizona	1; lack of records in N Cochise Co. until 1976 (Allen 1895, Roth and Cockrum 1976)
Sciurus aberti	NW in Colorado, N into Wyoming, W into Utah	Davis and Bissell (1989); known dispersal ability and history of ponderosa pine distribution (Davis and Brown 1989)
Baiomys taylori	N from SE Texas into Oklahoma, and NE in New Mexico	Diersing (1979); Stangl and Dalquest (1986); Taylor and Davis (1947) vs. Davis (1974); recent record in Luna Co., New Mexico (W. Gannon, personal communication); Choate et al. (1990)
Sigmodon hispidus	N in the U.S.; through Kansas to Nebraska, and N in Rio Grande Valley in New Mexico	Cockrum (1952); Mohlenrich (1961); Jones (1960); Cameron and Spencer (1981)
Sigmodon fulviventer	N in New Mexico	Mohlenrich (1961)
Sigmodon ochrognathus	NW in Arizona and N in Texas	Davis and Dunford (1987); Davis and Ward (1988); Davis et al. (1988); Hollander et al. (1990); Stangl and Dalquest (1991)
Microtus mexicanus	Various in Arizona; N in New Mexico into S Colorado	This study
Nasua nasua	NW in Arizona and perhaps in New Mexico	Not reported by early explorers (Davis 1982); not recorded in Arizona until 1892, in extreme S (Hoffmeister 1986); no late Pleistocene record (Harris 1985, Tabor 1940); Wallmo and Gallizioli (1954); but see Kaufmann et al. (1976)
Conepatus mesoleucus	NW in Arizona	1; recent records (Hoffmeister 1986)
Tayassu tajacu	N in Arizona and New Mexico	Indian name for peccary is of Spanish origin (Sowls 1984); rarely encountered by early explorers (Davis 1982); no use by early prehistoric cultures (Crosswhite 1984, Sowls 1984)

1938, and others prior to 1975, found no Mexican voles near Cimarron, New Mexico, although other vole species were taken (Armstrong 1972, Findley et al. 1975). The Mexican vole is now common in the area (Finley et al. 1986); thus, the northward range expansion by this species may be continuing into northeast New Mexico and southeast Colorado.

Discussion and Conclusions

The historical legacy hypothesis requires widespread late Pleistocene distribution. The fossil record documents the late Pleistocene presence of *Microtus mexicanus* in southern New Mexico, adjacent portions of Texas, and (perhaps) southeast Arizona. Despite the admittedly weak fossil record, however, there is no evidence that the species' range formerly included the entire area where populations now exist (Harris 1985). Several lines of evidence support post-Pleistocene dispersal for this species:

1. Distance as a predictor of presence/absence (Lomolino et al. 1989).
2. The close relationship of adjacent Arizona populations, isolated by theoretically crossable habitat.
3. Its presence in isolated habitats unlikely to have served as post-Pleistocene refugia.
4. Recent records suggesting dispersal in northwest and northeast Arizona, central and northeast New Mexico, and southern Colorado.

Although the distribution of the Mexican vole undoubtedly has been influenced by historical events and by local extinctions, it is difficult to ignore the evidence of past and continuing post-Pleistocene dispersal.

A reviewer of this paper asked why the Mexican vole and other small mammals took 4000 years to reach certain localities that we claim were colonized within the past few decades. This point requires clarification. First, there have been local changes in vegetation and climate in the Southwest during the past 50 to 100 years, and these conditions may have favored recent dispersal even though the broader picture has remained constant for some 4000 years. Second, we do not claim that these recent records represent the *first* colonizations by the Mexican vole or other species. They are simply the first such events that have been recorded in the literature. If these animals were able to cross unsuitable habitat once, then they could have done so repeatedly in the course of centuries.

Our suggestion of recent dispersal by the Mexican vole should be evaluated in the context of a more general pattern involving many mammal species. Post-Pleistocene dispersal has influenced montane species assemblages throughout much of the Southwest (Lomolino et al. 1989). In addition, we propose a second pattern of recent northward range expansion involving at least 19 North American mammal species, all primarily austral in distribution but occupying a wide range of habitats (Table 1).

This pattern of northward dispersal is not easily explained, and there is unlikely to be a single causative factor. For some species, the shift appears to result from climatic change and/or habitat modification by humans. Alternatively, the pattern can be viewed as one small, recognizable northward surge in a continuing Holocene cycle of north/south distribution shifts.

Acknowledgments

Preliminary drafts of the manuscript were read by R. Sidner, M. V. Lomolino, and E. L. Cockrum. T. Van Devender and an anonymous reviewer also provided helpful comments. Some of the fieldwork cited was conducted by R. B. Spicer and C. LaRue with support from the Arizona Department of Game and Fish.

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Received 12 October 1990
Accepted 17 June 1992